Ecological connectivity analysis to reduce the barrier effect of roads. An innovative graph-theory approach to define wildlife corridors with multiple paths and without bottlenecks

Manuel Loro

Emilio Ortega

Rosa M. Arce

Davide Geneletti

1. Introduction

The fragmentation of ecosystems, and especially the loss of connectivity between different habitat areas, is considered to be one of the main impacts on biodiversity caused by linear transport infrastructure and is also known as the barrier effect to wildlife dispersal movements (Cuperus, Canters, & Piepers, 1996; Forman & Alexander, 1998). The prediction of the impacts of the barrier effect when defining a road layout is one of the main deficiencies in the planning of these projects in environmental impact studies (Geneletti, 2006), in addition to the scarcity or absence of studies enabling the correct and exact location of wildlife crossing (Gurrutxaga & Saura, 2014; Loro, Arce, Ortega, & Martín, 2014; van Bohemen, 1998).

Ecological connectivity models are used to quantify habitat patches and the role of wildlife and can therefore be incorporated to

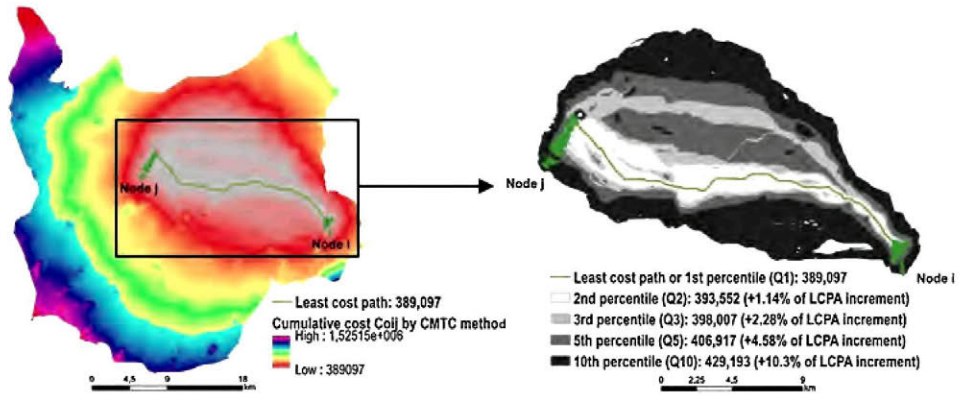

Fig. 1. Main differences between existing and proposed methodology. Cumulative cost distance raster for a pair of nodes *ij* ($CCDR_{ij}$), see left. Proposed reclassifying methodology by Theobald et al. (2006), see right. In this example, output provided by Q10 threshold value is similar to original CMTC methodology (Pinto & Keitt, 2009).

prevent the barrier effect during the decision-making phase in the spatial planning of linear infrastructures (Geneletti, 2004). These models can also help locate areas in which to promote the restoration or creation of new habitats as compensatory measures (Found & Boyce, 2011). Landscape characteristics can strongly constrain the dispersal of wildlife corridors associated to these processes (Pinto & Keitt, 2009), especially when they will be altered by new construction.

In this context, graph theory allows the landscape to be simplified into a habitat network composed of key elements defined as a set of nodes (optimal habitat patches for certain species) which are connected by arcs or links (wildlife corridors) in order to study their functional connectivity on a regional scale (Bunn, Urban, & Keitt, 2000; Tischendorf & Fahrig, 2000; Urban & Keitt, 2001). One of the challenges of graph theory is to determine the likelihood of wildlife using each link, i.e. the frequency of movement between habitat patches that connects nodes. One of the most commonly applied methodologies is the use of cumulative cost distance functions to calculate the least-cost path (Dijkstra, 1959) and later transform it to probability values, especially for modeling wildlife movement patterns based on a prior knowledge of the landscape. Several examples can be found in the literature (Bunn et al., 2000; Drielsma, Manion, & Ferrier 2007; Gurrutxaga, Rubio, & Saura, 2011; Pereira, Segurado, & Neves, 2011; Yu, Xun, Shi, Shao, & Liu, 2012). Tools such as *Pathmatrix* (Ray, 2005), *Matrix Green* (Bodin & Zetterberg, 2010), *Graphab* 1.0 (Foltête, Clauzel, Vuidel, 2012) and *Cost Distance Matrix* script for *ArcGIS* 10 (ESRI, 2010) have been developed to automate the probability calculation for a large number of links in a landscape graph network based on the calculation of the least-cost path between each pair of nodes.

Although the results obtained with the least-cost path (*LCPA*) as input seem to be robust in sensitivity analyses designed to predict patch occupancy and inter-patch movements (Girardet, Foltête, & Clauzel, 2013; Rayfield, Fortin, & Fall, 2010), some authors question their use for defining links in connectivity studies for two main reasons (Adriaensen et al., 2003; Beier, Majka, & Spencer, 2008; Cohen, Amit-Cohen, Cohen, & Shoshani, 2009; Majka, Jenness, & Beier, 2007; McRae, Dickson, Keitt, & Shah, 2008). The first problem (P1) concerns the fact that animals present some randomness in choosing one corridor over another and do not only use the lowest cost distance corridor defined by *LCPA* methodology. The second problem (P2) with the use of *LCPA* to define corridors is the lack of definition in the corridor width, since they are represented by a single line.

The result of the first problem (P1) is that a link will not be defined by all the potential paths connecting a pair of nodes considered in the analysis, especially when they may have a similar cost to the one generated by *LCPA*. This can lead to an overestimation of the ecological importance of that link because only the path with the least cost is selected, and none of the other paths which may also be fairly representative of that link. The second problem (P2) undermines the quality and utility of a territorial planning process, as the wildlife corridor is defined only as a single least-cost path without boundaries, which adds a high degree of inaccuracy to the analysis (Drielsma et al., 2007; Zetterberg, Mörtberg, & Balfors, 2010), as pointed out by the latter authors. The intersection of two corridors connecting different pairs of nodes will produce only one point, which has little ecological and planning significance.

The literature contains some methodologies that seek to solve these two problems when defining links. Adriaensen et al. (2003) suggested an iterative programming operation of Dijkstra's algorithm to obtain different least-cost paths for a pair of nodes. Pinto and Keitt (2009) proposed the Conditional Minimum Transit Cost (*CMTC*) methodology which defines a corridor that connects a pair of nodes by multiple paths with a similar cumulative cost distance value (see Fig. 1). The first step in *CMTC* is to calculate a cumulative cost distance raster (*CCDR*) for a pair of nodes *ij* (Co_{ij}) as the combination of the cumulative cost distance (also known as effective distance) from node *i* (C_i) and node *j* (C_j). The second step is to reclassify the Co_{ij} into two cluster groups: the included and excluded group according to the threshold value of Co_{ij} distribution defined by the user. This methodology solved both *LCPA* problems (P1 and P2), but added three new challenges: (ch1) what is the best threshold value from a statistical and ecological point of view? (ch2) How can paths with bottlenecks be massively excluded? (ch3) What is the threshold value at which at least one path is achieved without bottlenecks between a pair of nodes?

In response to the first challenge (ch1), several authors have proposed methods to define the reclassifying threshold value (Beier et al., 2008; Majka et al., 2007; Pinto & Keitt, 2009; Theobald, Norman, Sherburne, 2006; Zetterberg et al., 2010). For instance, Pinto and Keitt (2009) proposed a 10% increment in the cost values in the least-cost path to obtain multiple paths for the pair of nodes, although they recognized the randomness of this value. Likewise in Theobald, Crooks, and Norman (2011) and Theobald, Reed, Fields, and Soulé (2012) the authors used *FunConn* tool (Theobald et al., 2006) to define corridors according to the *n*th percentile of the Co_{ij} distribution. *FunConn* tool users must select the most statistically representative percentile as a threshold, although there is still a degree of randomness as to which *n*th percentile must be selected. A similar approach was proposed by McRae et al. (2008), who considered the landscape as a circuit system in which nodes are connected by special links made up of one or more resistors (also known as circuit theory).

These methodologies define the corridor connecting two nodes by multiple paths (challenge ch1) or branches of similar cumulated

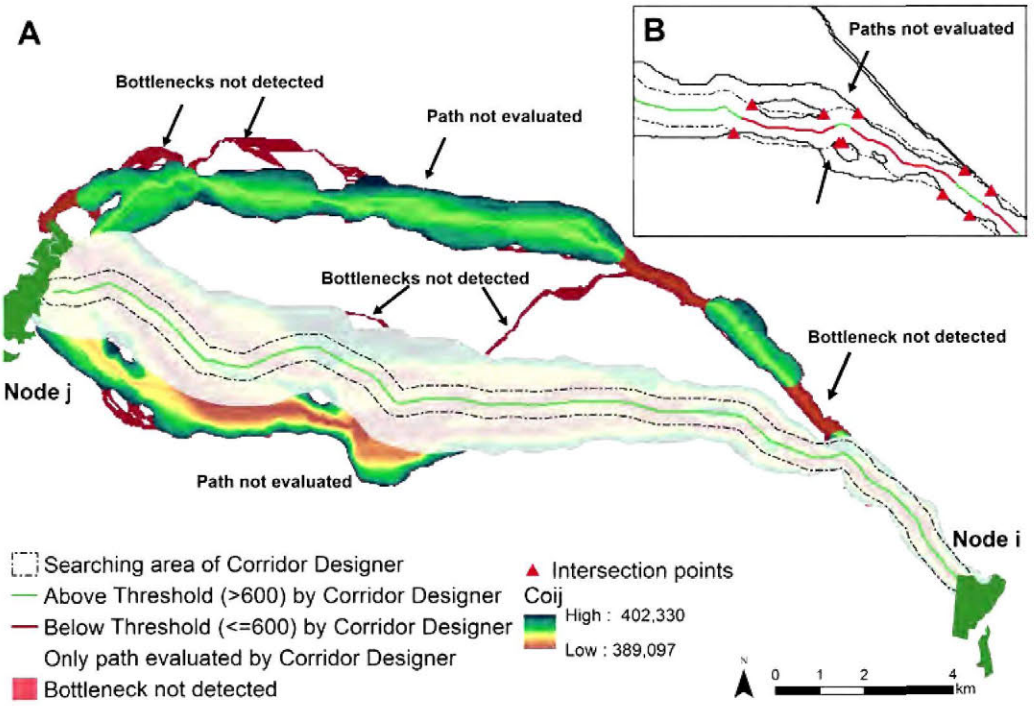

Fig. 2. Output results provided by Corridor Designer Tool (Jenness, Majka, et al., 2011; Jenness, Brost, et al., 2011), highlighting its limitations in evaluating part of the multiple paths in corridor *ij*. (B) Detailed map of how Corridor Designer Tool works. Once the centerline of the widest possible sections of the corridor polygon is defined, intersection points between searching area and corridor locate the narrow part.

cost distance (or electrical resistance), but do not resolve either of the other challenges (ch2 and ch3). As can be seen in Fig. 1 where we applied the *FunCoon* tool methodology to a pair of nodes for illustrative purposes, choosing a low threshold value (e.g. Q3 which is 2.28% of the *LCPA* increment) produces several multiple paths, but many are too narrow (ch2 unsolved) and – if not excluded – could overestimate their connectivity function (ch3 unsolved). Furthermore, because there is regularly an increment of 1.14% between two consecutive percentiles, we have omitted the study of threshold values with a lower cost percentage or change in interval range, as this would not be sufficiently detailed and underestimate a better solution located between Q2 and Q3, for instance (ch3 unsolved).

In order to detect the presence of bottlenecks in a corridor, Jenness, Majka and Beier (2011) developed the *Corridor Designer Evaluation Tools* to exclude corridors outside a value of geometrical width defined by the user. The main limitation of this tool is that it only enables the analysis of one path in a corridor composed by multiple paths. As can be seen in Fig. 2, only the path that goes through the center of the widest possible sections of the corridor polygon is evaluated (Jenness, Majka, et al., 2011; Jenness, Brost, & Beier, 2011), but none of the other multiple paths with a similar Co_{ij} value. Challenge ch2 is thus only partially solved.

The aim of this paper is to present a new graph theory approach for landscape that defines links by multiple paths that connect a pair of nodes and ensures that: (1) a corridor's multiple paths defined by different threshold values give significant differences between them in the *CCDR* raster distribution; (2) the iterative search process ends only when at least one path has no bottlenecks; and (3) all the multiple paths or branches located in a corridor that connect a pair of nodes will be assessed. Similarly to Theobald et al. (2011, 2012), we also assume that the reclassifying of the Co_{ij} raster distribution is helpful to obtain corridors composed of multiple paths, although our classification method differs from theirs in that we choose natural breaks as they are statistically more representative than percentiles. This system is more effective for grouping together similar values, and maximizes the differences between classes (natural breaks are explained in Section 2.2). Another difference is that we vary the classification threshold value iteratively until we find an operative path that really connects the pair of nodes without bottlenecks. In this process, unlike Jenness, Majka, et al. (2011) and Jenness, Brost, et al. (2011), all – not only part – of the multiple paths of a corridor are assessed.

To illustrate the usefulness and effectiveness of our proposed methodology – designated Conditional Minimum Transit Cost without bottlenecks (*CMTC_wb*) – we assess the potential contribution of nodes and links to landscape connectivity, where links were defined both by the least-cost path and our methodology to compare both methodologies. This approach studies the effects of habitat network structure on functional dispersal processes, and thus the way in which nodes and links are defined will condition whether the habitat graph really represents the functional connectivity between habitat patches. Recent literature reviews on network analysis of landscape connectivity and measures include Baranyi, Saura, Podani, and Jordán (2011); Blazquez-Cabrera, Bodin, and Saura (2014), or Rayfield, Fortin, and Fall (2011).

In order to assess and compare the connectivity of each node and link using both as inputs, we selected the possibility of connectivity index (Saura & Pascual-Hortal, 2007) as a connectivity metric to measures the different ways each landscape element can contribute to overall habitat connectivity at the landscape scale.

Specifically, the study was conducted in a heterogeneous landscape where a new freeway was being planned and where roe deer is considered to be one of the most sensitive species to ecological fragmentation. This analysis allowed the identification of potential sites for wildlife crossing and habitat restoration in order to reduce the damage to connectivity between habitat patches within each alternative section of freeway in the planning stage. Thus by improving the definition of links, this research could have significant practical implications for the calculation of landscape connectivity metrics based on graph theory, and contribute to more sustainable planning of linear infrastructures such as roads.

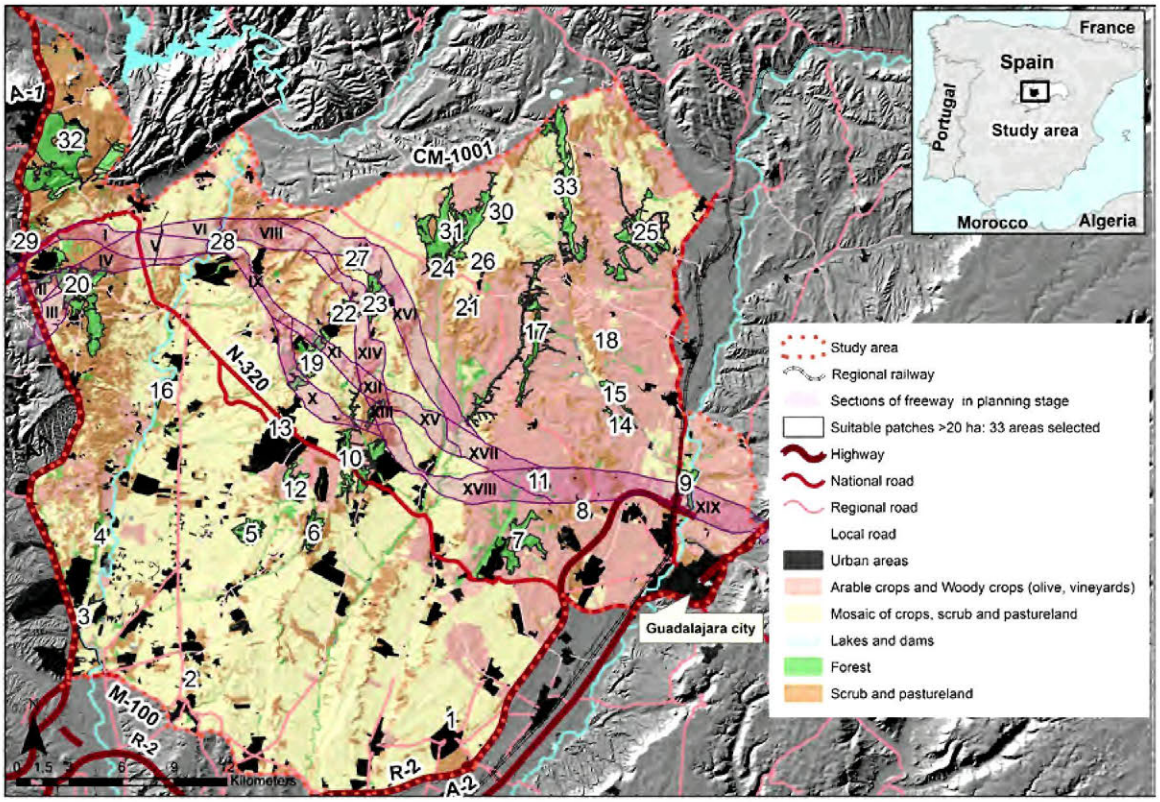

Fig. 3. Location of the study area.

2. Materials and methods

2.1. Study area and focal species selection

Our study area is located in the central Iberian Peninsula in southwest Europe. The boundaries of the study area were established based on barriers (freeways, national and regional roads with high traffic levels) which prevent or reduce the movement of wildlife between different forest patches. The landscape in the study area is characterized by isolated patches of forest that support ecological connectivity for large mammals and is the site of a planned freeway corridor that could modify this connectivity. The area is hilly and has a mosaic structure with patches of Mediterranean oak forests (*Quercus pyrenaica Willd.* and *Quercus ilex L. subesp. ballota*), pine forests (*Pinus nigra subsp. salzmannii var. salzmannii*), scrubland, low-growing woody and rainfed crops and urban areas (see Fig. 3). The Ministry of Public Works is planning a new freeway to connect the existing A1 and A2 roads (Ministerio de Fomento, 2006). This infrastructure has been divided into nineteen sections that could constitute alternative freeway corridors to accurately assess the ecological impact of each alternative road corridor.

Roe deer was selected as the study species as it is the large mammal with the most numerous presence in the study area according to the Spanish Inventory of Land Species (Ministerio de Medio Ambiente, 2007), a 10 km × 10 km grid that certifies the presence of individuals based on droppings and footprints. We considered roe deer as an umbrella species for others species in our case study (red deer and wild boar), meaning that the conservation of this species also confers protection on a large number of other species that coexist in the study area (MARM, 2010).

2.2. Construction of the habitat model

The habitat preferences of roe deer were considered in order to simplify the landscape into a graph network (Urban & Keitt, 2001). Following a literature review (Beier et al., 2008; Bentrup, 2008), four criteria were chosen to locate potential nodes (focal areas) where roe deer could rest during the daytime: (c1) minimum forest cover of the habitat patch; (c2) minimum patch size (see Table 1); (c3) patch core area (undisturbed area with high proportion of natural vegetation characterized by the absence of edge effects extending from surrounding areas); and (c4) level of connectivity of the patches. These four criteria were adapted to existing habitat models for roe deer populations in Spain based on the results of tracking roe deer by various authors (Acevedo et al., 2010; Mateos-Quesada, 2005; Torres, Virgós, Panzacchi, Linnell, & Fonseca, 2012).

The literature review showed that for the first criterion (c1) the presence of roe deer was higher in patches with a forest canopy cover ≥70%. For the second criterion (c2), we followed Schadt et al. (2002) who proposed assuming a relationship between density and patch size in order to select nodes in connectivity analysis. Considering that Mateos-Quesada (2005) found an optimum density of 4.24 individuals per 100 ha in broad-leaved forest and 1.69 individuals per 100 ha in pine forest in the central Iberian Peninsula, a single male individual (which has a solitary behavior for part of the year) would require 20 and 50 ha respectively (for more details, see Table 1). For criterion c3, forest patches of less than 500 m wide were not selected as nodes even if they satisfied the conditions of minimum area, in order to ensure a core area. Fragmented patches were considered connected and suitable for home ranges if forest patches were separated by less than 100 m (criterion c4). This distance was chosen based on a sensitivity analysis with different distances to aggregate patches close to a single node. We found that for distance values lower than 100 m, the corridors with the highest connectivity value were located between nodes that were very close. Since these nodes were separated by roads with low traffic (local roads) and rainfed crops, and taking into account the crepuscular behavior of roe deer, we considered the animals could easily cross between patches in close proximity. By simplifying the

Table 1
Median natal dispersal distance (D) calculated from the optimal density of roe deer and release data in various landscapes on the Iberian Peninsula.

Landscape	Optimal density (individual/100 ha)	Source	Optimal habitat area[a] (ha)	Median dispersal distance, D^b (m)	Maximum dispersal distance[b] (m)
Broad-leaved forest. Oak forest (*Quercus pirenaica Willd.* y Quercus *ilex* subsp. *Ballota* L.)	4.24	Mateos-Quesada (2005)	20	3131	17,888
Pine forest	1.69	Mateos-Quesada (2005)	50	4949	28,284
Broad-leaved forest	3.4	Costa (1995), cited in Mateos-Quesada (2005)	25	3500	20,000
Pine forest	2.6	Costa (1995), cited in Mateos-Quesada (2005)	38.5	4341	24,806
Mixed pine and oak forests. Cropland and pine forest mosaic	5.56	Acevedo et al. (2010) López-Martín, Martínez-Martínez and Such (2009)	18 –	2970 2800 (data observed by the authors)	16,970 18 (data observed by the authors)

[a] Obtained by transforming the optimum density size of roe deer per 100 ha to ha per single individual based on the behavior of single male roe deer.
[b] Obtained based on the transformation of optimum habitat patch size for a species to median and maximum dispersal distance proposed by Bowman, Jaeger, and Fahrig (2002), who define median dispersal distance as seven times the square root of the optimum species area.

connectivity graph with more separate nodes we were able to obtain longer corridors and a higher presence in the study area, implying a greater potential impact by the new freeway. Finally, 33 nodes (n) were selected as sources of dispersal movements of roe deer in the study area (step 1, see Fig. 4).

Since our objective was to generate a link composed of multiple paths with similar cost values instead of a least-cost path single line, we programmed two python scripts based on GIS tool routines for ArcGIS 10. These scripts were run with *Pythonwin* 2.6 (Hammond, 2010). The first script was designated *Generator of Alternative Corridors (GAC)*, as it allows users to define several alternative dispersal routes with a lower accumulative cost distance for each pair of nodes. The second script, *Narrow Corridor Eraser (NCE)*, enables users to delete routes previously defined by *GAC* that do not meet a

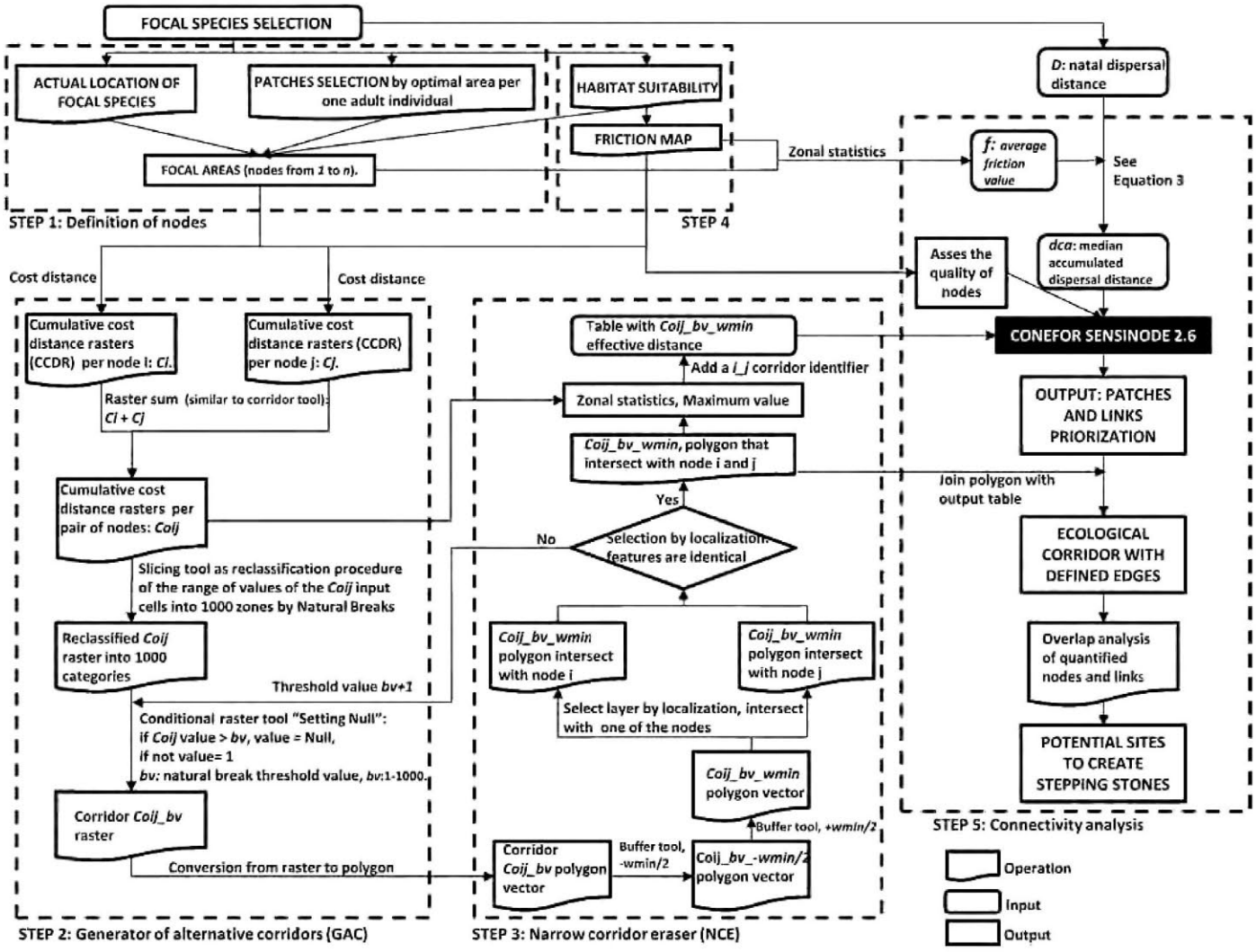

Fig. 4. The flow chart shows the procedure used to assess connectivity for roe deer in the study area. Two GIS methodologies were used to identify potential ecological corridors without bottlenecks considering roe deer behavior and landscape.

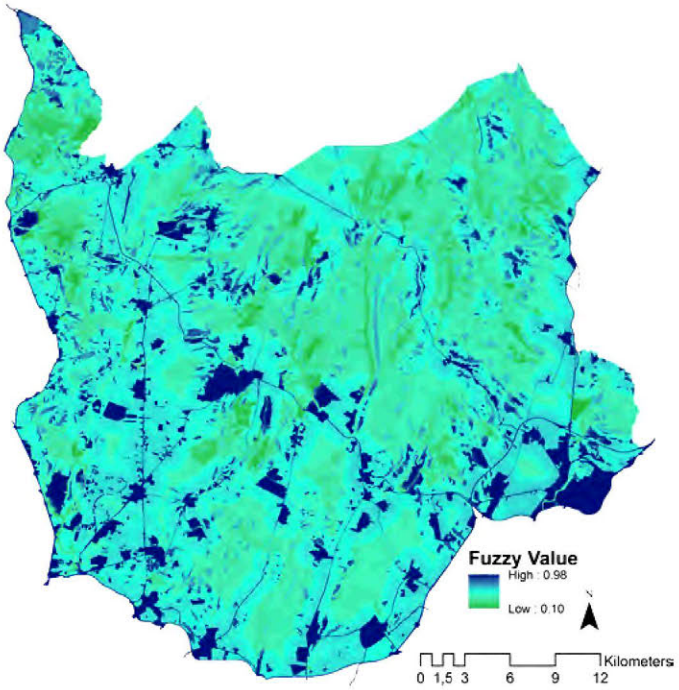

Fig. 5. Relative cost raster after applying the fuzzy gamma operator as an aggregation tool with a coefficient gamma value of 0.9. Land-use information was obtained from thematic maps (MARM, 2007; Ministerio de Agricultura, 2010; Ministerio de Fomento, 2005) and wildlife species distribution (Ministerio de Medio Ambiente, 2007).

geometric minimum width for wildlife requirements (steps 2 and 3, see Fig. 4).

Previously, we defined a friction map or relative cost raster for roe deer dispersal movements from a review of the literature on roe deer mobility and habitat use (step 4, see Fig. 4). Selected factors were land uses (assessed by degree of naturalness, food source potential, ability to hide roe deer movements and act as partial barriers to dispersal movements), influence of proximity to elements that condition animal behavior (such as transitional zones between patches, attraction effect of water resources, or potential disturbance effects of proximity to human-modified areas) and landforms. A sensitivity analysis of cost values assigned to each factor was done by aggregating them using the fuzzy operator Gamma with gamma coefficient values from 0.1 to 0.9, where resistance could take values between 0 (low resistance) and 0.98 (high resistance), see Fig. 5.

Below, we describe the operations of GAC and NCE tools in detail.

2.2.1. Generator of alternative corridors (GAC)

The Co_{ij} cumulative cost distance raster was generated by adding the relative cost raster (C_i and C_j) of each pair of nodes ij which are connected by a link (step 2, see Fig. 4). As can be seen in the example shown in Fig. 6, Co_{ij} pixels with lower values are located close to the least-cost path. Contiguous to them are other pixels with lower values as alternative paths connecting the pair of nodes. Depending on the minimum corridor width value selected by the user, different multiple paths can be found for a single corridor. Following some authors' recommendations (Adriaensen et al., 2003; Beier et al., 2008) when selecting a representative cost threshold value, we ran a reclassification iteration operation to generate alternative corridors with different widths.

A raster reclassification process of Co_{ij} was performed based on the natural breaks classification method (Jenks, 1967). This process reclassifies the range of values of the Co_{ij} raster into different intervals. It reduces the variance within intervals and maximizes

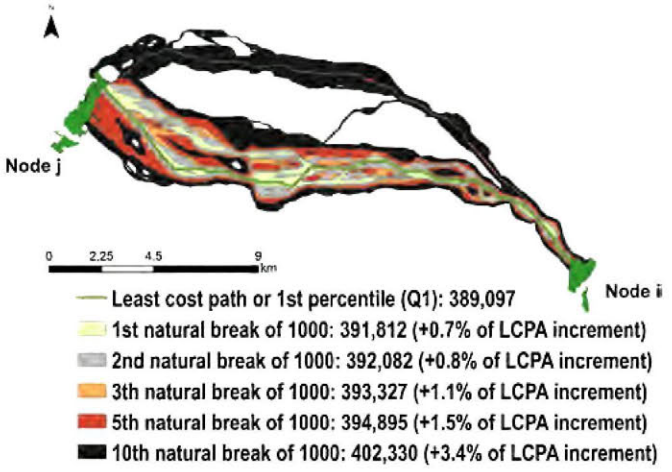

Fig. 6. Output results provided by proposed methodology in this paper. Results given here are from the slicing tool, later reclassified as natural break points in the distribution of values in the Co_{ij} raster. Only corridors obtained for threshold values of natural breaks $bv = 1$, 2, 3, 5 and 10 (Co_{ij}_1, Co_{ij}_2, Co_{ij}_3, Co_{ij}_5 and Co_{ij}_10) are shown as an example in the figure.

the variance between intervals as it seeks to minimize the average of each interval deviation from the class mean, while maximizing each interval deviation from the means of the other intervals (Jenks, 1967). We selected this reclassification methodology to highlight where there are significant variations in the Co_{ij} distribution. To obtain a detailed evaluation of each Co_{ij}, the cost distribution value was split into 1000 natural break points (bv). With this number of natural break points, Co_{ij} accumulated cost variations were less than 1% between two consecutive intervals in our case study. Fig. 6 shows several links of increasing width obtained for intervals $bv = 1$st, $bv = 2$nd, $bv = 5$th and $bv = 10$th.

2.2.2. Narrow corridor eraser (NCE)

Once the Co_{ij}_bv was generated (see Fig. 7A), it needed to be checked to remove possible bottlenecks generated during the *GAC* process. The minimum geometric width (defined as *wmin*) of a wildlife corridor must be established to ensure that human activities localized around it do not significantly affect the animals, as they might not use the corridor (Jenness, Brost, et al., 2011). In our case, we chose a minimum width of 600 m (*wmin*) as a recommended general minimum value to maintain the functionality of the wildlife corridors (Beier et al., 2008; Kennedy, Wilkinson, & Balch, 2003).

A double transformation process was done to Co_{ij}_bv with the buffer tool (step 3, see Fig. 4). Initially, a negative buffer of $-wmin/2$ was applied to reduce the corridor size to half the minimum geometric width (see Fig. 7B). A positive buffer of $+wmin/2$ was then applied to recover the original size of the corridor (see Fig. 7C). During this operation to reduce and recover the original size of the corridor, any part of the corridor presenting bottlenecks did not recover its original size in those parts, thereby retaining only the wildlife corridors without bottlenecks. We tested whether the output corridor maintains the connection between both nodes i and j. If they were identical, it means the connection was maintained. If not, Co_{ij}_bv was excluded and the process started again with the next ith $bv+1$ natural break in the *GAC* process. The process was repeated iteratively with the next ith $bv+1$ natural break until a corridor were obtained without bottlenecks and maintaining the connection between both nodes ij (see Fig. 7D). This corridor link was designated $Co_{ij}\_bv\_wmin$. An example of this process can be seen in Fig. 7, where Co_{ij}_10 was finally selected as the reference corridor as it satisfied the condition of having no bottlenecks in at least one of its multiple paths. In the case of Co_{ij}_5 and Co_{ij}_7, no

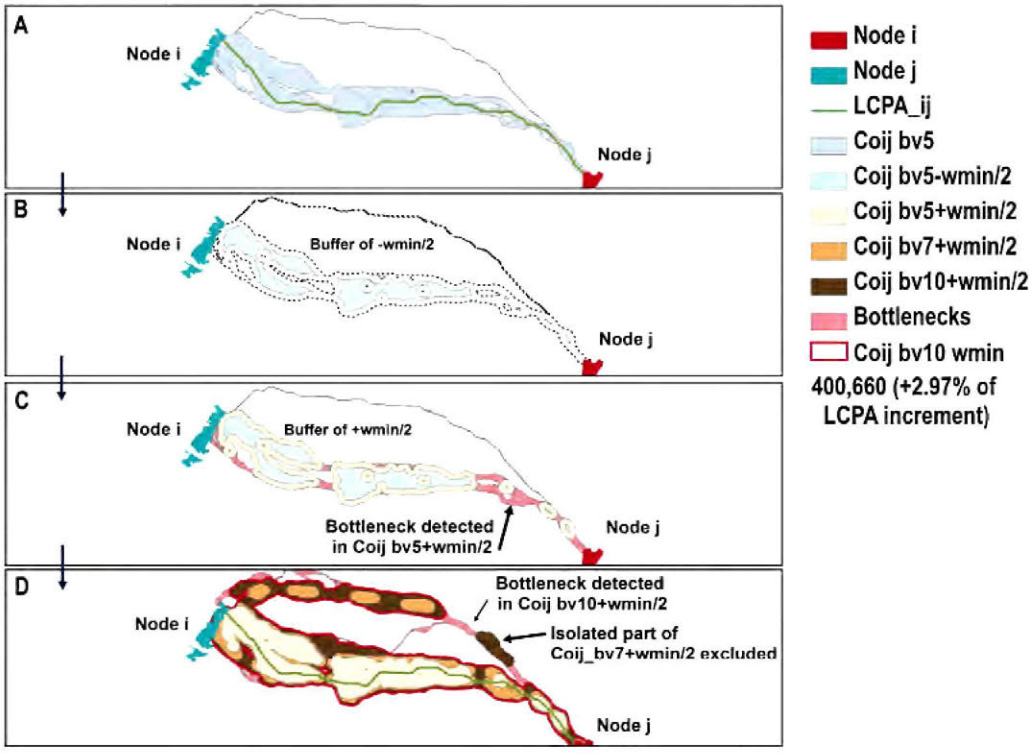

Fig. 7. Graphic example of the iterative combined *GAC* and *NCE*. (A) Corridor Co_{ij}_bv5 generated by *GAC* defines the threshold value interval in the 5th natural break. (B) The size of corridor Co_{ij}_bv5 is reduced by a buffer of *−wmin/2*, where *wmin* is the minimum geometric width admitted for a wildlife corridor. In this process, sections of paths with bottlenecks are removed. (C) Corridor Co_{ij}_bv5-wmin/2 size is increased by *+wmin/2*. Only paths or sections of paths without bottlenecks can be recovered. (D) Corridors Co_{ij}_bv5 or Co_{ij}_bv7 failed to maintain the connection between nodes after NCE was applied. Both corridors were discarded and the iterative process continued up to Co_{ij}_bv10 (+2.97% of *LCPA* increment) where connectivity between nodes was assured.

path fulfilled the required criterion of no bottlenecks. Indeed, in our case study, the most frequent threshold values for obtaining a corridor without bottlenecks were the 7th and 9th natural breaks out of 1000 (see Appendix A, Fig. S1).

Once the polygon Co_{ij}_*bv_wmin* was defined, it was characterized by the maximum cumulative cost distance value (which conditioned the link width) through a zonal statistic operation with the Co_{ij} raster (see Fig. 4, Step 3). Finally, the corridor identification codes were also included in Co_{ij}_*bv_wmin* with the nodes *i* and *j* (see Section 2.3).

2.3. Connectivity analysis

The connectivity of the graph network was assessed using the possibility of connectivity index (*PC*) developed by Saura and Pascual-Hortal (2007). The *PC* index indicates the probability of two roe deer randomly placed in our study area occurring in habitat patches that are reachable from each other (Saura & Pascual-Hortal, 2007). This index has been used successfully for landscape planning and species conservation studies (Bodin & Saura, 2010; Carranza, D'Alessandro, Saura, & Loy, 2012; Ng, Xie, & Yu, 2013) and to predict the effect of road networks on landscape connectivity (Fu, Liu, Degloria, Dong, & Beazley, 2010; Gurrutxaga et al., 2011; Vasas, Magura, Jordán, & Tóthmérész, 2009).

As shown in Eq. (1), this index can be classified as an area-based functional metric (Ng et al., 2013) which incorporates suitable habitat areas in origin and destination patches (weighted by node habitat value for the focal species), connected by wildlife corridors (or links):

$$PC = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} a_i \cdot a_j \cdot p_{ij}^{*}}{A_L^2} \quad (1)$$

where, a_i and a_j are suitable habitat areas for roe deer inside patches *i* and *j* respectively, weighted by their habitat quality; A_L is the total landscape area, weighted by the highest habitat quality assigned in the study; and p_{ij}^{*} is the maximum product of dispersal probabilities along the links of all possible paths between nodes *i* and *j*.

As proposed by Saura and Rubio (2010), for a better understanding of the role played by each *k* key element in the global connectivity, an iterative analysis of the relative variation of the *PC* index (defined as δPC_k) was performed before and after the removal of one single element. These authors recommended partitioning δPC_k into three fraction indexes following the equation:

$$\delta PC_k = \delta PCintra_k + \delta PCflux_k + \delta PCconnector_k \quad (2)$$

where $\delta PCintra_k$ is the contribution of each habitat patch (node) *k* according to its size and ecological quality to the overall connectivity; $\delta PCflux_k$ is the contribution to the dispersal movement or flux generated by one patch *k* due to its intrinsic attributes (habitat area and habitat quality) and its topological position relative to the other patches (as generator or receptor of flux); and $\delta PCconnector_k$ is the contribution of a patch or link *k* to the connectivity between other patches in terms of its topological position, not area. In the case of links, this contribution is only recorded for certain links that belong to the best (maximum product probability, p_{ij}^{*}) path for dispersal between other patches *i* and *j*, and weighted by the ecological importance of the nodes that connect them according to area and habitat suitability. The nodes can function as stepping stones located on the best path connecting patches *i* and *j*, contributing as a complementary element to link *k*.

Our connectivity analysis through the index δPC_k and its fractions involved three steps (step 5, see Fig. 4). The first step was to calculate the internode direct dispersal probability for roe deer in the study area. A conversion factor (θ) of cumulative cost

distance to probability was calculated following the adaptation of Gurrutxaga et al. (2011) to the negative exponential decay function (Bunn et al., 2000; Hanski, 1999), which originally only used the Euclidean distance between nodes:

$$p_{ij} = e^{-\theta \cdot dca_{ij}}, \quad \text{where} \quad dca = d_{ij} \cdot \bar{f} \tag{3}$$

where θ is the conversion factor to transform cumulative cost distance to probability of migration or dispersion p_{ij} in a certain Euclidean distance from a node i to a node j (or vice versa). In our case study a median dispersal distance ($p_{ij} = 0.5$) was defined as a calculation reference as suggested by Saura and Pascual-Hortal (2007). *dca* is the effective distance or accumulated cost distance, d_{ij} is the median Euclidean dispersal distance (in meters) that a focal species can move through a homogeneous map unit defined as a reference (land uses, location, population behavior) and $\bar{f}$ is the average value of cost friction in those homogeneous units defined as a reference in our case study. We chose optimum habitat patches for roe deer as this was the only reference found between Euclidean dispersal distances and land-use characteristics (see Table 1). This value was **13.1** in our case study and was calculated with a zonal statistical analysis over node polygons. The ecological significance of this adaptation of Gurrurtxaga et al. (2011) is that the more distant the nodes to be reached by a species, the more similar the matrix to be crossed to these optimum habitat nodes.

Different dispersal distances ($d_{ij} = 0.5$, 1, 3.5, 5, 10, 15, 20 and 25 km) were selected and evaluated to perform a sensitivity analysis showing how the probability of corridors changed and whether they could potentially be used by roe deer. In this process, a different θ conversion factor was obtained for each d_{ij} according to Eq. (3).

In the second step, after defining the θ conversion factor, the cumulative cost distance of each corridor without bottlenecks $Co_{ij}\_bv\_wmin$ (see previous Section 2.2) was transformed to probability values (p_{ij}), and δPC_k and its fractions were calculated for different d_{ij} values. All the calculations were performed with *Conefor* 2.6 *Sensinode and Sensilink* (Saura & Torné, 2012) using prioritization and *leave one out* ranking procedures (Saura & Rubio, 2010).

In the third step, we detected overlapping areas between corridors that connected different pairs of nodes and intersected. To quantify and map these areas, nodes and $Co_{ij}\_bv\_wmin$ corridors which were individually characterized by the $\delta PCconnector_k$ value obtained in step 2 were rasterized and added together. We assumed that crossover areas between corridors had the same connectivity importance as their sum and thus had a higher value in maintaining global connectivity than a single corridor.

In addition to the analysis of connectivity to define the link probability (p_{ij}) with our proposed *CMTC_wb* methodology, we made the same analysis with the least-cost methodology in order to compare the results (see Section 3.4).

3. Results

3.1. Overall landscape connectivity in the study area

The habitat distribution and the connection zones between focal areas were assessed in 33 nodes (n) and 528 links, since $n(n-1)/2$ is the number of links in an undirected complete graph with n nodes (Saura & Torné, 2012). The relative contribution of each δPC_k fraction ($\delta PCintra_k$, $\delta PCflux_k$, $\delta PCconnector_k$) was different for each natal dispersal distance. For values of median dispersal distance $D < 2.5$ km, $\delta PCintra_k$ had a contribution to the overall connectivity of between 90% and 40% (see Appendix A, Fig. S2). Distance values $D > 2.5$ km, $\delta PCflux_k$ made a significant contribution to global connectivity (δPC).

In the case of $D = 3.5$ km, a disaggregated analysis of $\delta PCconnector_k$ values showed 13.4% overall connectivity (δPC) from links and 5% from nodes (as stepping stones), achieving the maximum $\delta PCconnector_k$ value for our study (see Appendix A, Figs. S2 and S3). This threshold value was actually close to the estimated range of 3–5 km as a reference median dispersal distance for roe deer in the central Iberian Peninsula in our literature review (see Table 1). We chose this value as a reference threshold value for the rest of our analysis (see Section 3.1) as it ensures that species dispersal movements are based on intermediate stepping stones and links (high $\delta PCconnector_k$ values), and the landscape is therefore more sensitive to landscape fragmentation (Bodin & Saura, 2010; Saura & Rubio, 2010).

3.2. Importance of certain links and nodes to global connectivity

The relative importance of each network element for the dispersal distance considered ($D = 3.5$ km) was found in two areas with node values of δPC ranging between 12 and 25% (see Appendix B). One zone is located to the NW of the graph, where nodes 20 and 32 have the highest values of δPC through being well-connected via node 29, which acts as a stepping stone since it has the highest value of $\delta PCconnector$ for a node in the entire graph. Another important zone is in the NE of the graph and comprises nodes 10, 19, 25, 31 and 33, as the reference highest δPC patches in the landscape.

The δPCflux fraction had the highest values of all nodes with the exception of node 32. $\delta PCconnector$ provided by the nodes was higher than 1% in nodes 22, 29, 31 and 33 – implying that they acted as stepping stones – while $\delta PCintra$ never exceeded 7% in any of the nodes, except in node 32 ($\delta PCintra = 16\%$; Appendix B). Node 32 had the highest contribution to overall connectivity ($\delta PC = 25.59\%$), but because of its larger size (1159 ha) and lateral position in the graph, the $\delta PCflux$ fraction was lower than the $\delta PCintra$ fraction.

An analysis of wildlife corridors showed that 31 out of 528 links had a δPCconnector value higher than 0.1% (see Figs. 8 and 9); and of these, only three had values above 3.5%, including their values with and without overlapping (links: 20_29, 25_33 and 29_32). These links all provided the connection between large size and lateral nodes (e.g. nodes 25 or 32) and central nodes which acted as stepping stones in the graph (e.g. 29 or 33). Link 20_29 connected the most important stepping stone (node 29) to node 20, which in turn acted as a relatively important stepping stone between the NW and NE zones of the graph.

As a result of the connectivity analysis with inputs provided by the *CMTC_wb* methodology, the overlapping calculations showed important variations of $\delta PCconnector$ related to the links. Depending on whether the mean or maximum connectivity values were compared in each corridor, important variations were found for links 10_17 and 19_22, together with relatively high values of $\delta PCconnector$ (see Fig. 9). As a result of the overlapping calculations of these two links, the pixel values of $\delta PCconnector$ were found to be locally higher than the mean value due to the high density of links concentrated in this area. These results underline the high potential of these pixels to create a new optimal area as a stepping stone patch. Similar situations can be found for other links (e.g. 10_19; 10_22; 10_31).

3.3. Analysis of planned freeway sections

As a result of our connectivity analysis of nodes and links (Sections 3.1 and 3.2), the potential fragmentation of various planned freeway sections could be assessed in more detail (see Fig. 10). We found that section I would affect link 20_29, but due to the narrow road section in this area and the Santa Lucia creek, the potential construction of a viaduct or oversized bridge could serve as a wildlife passage.

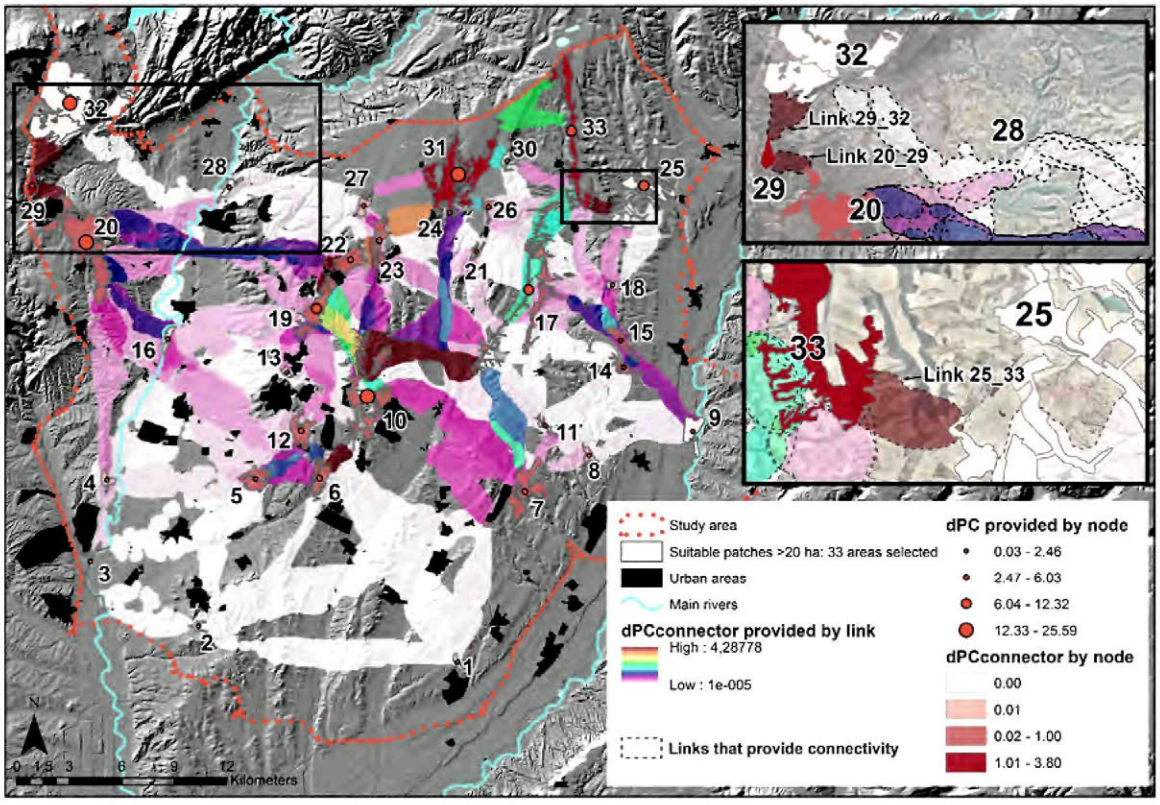

Fig. 8. Output links with $\delta PC_{connector}$ values > 0.1%. In addition, δPC and $\delta PC_{connector}$ values provided by nodes are shown for 3.5 km as the reference median dispersal distance (D).

Freeway sections XI, XII and XV run parallel to link 10_17, and it would not be feasible to locate a wildlife passage there as it is not perpendicular to the layout of the alternative. In contrast, although sections XVI and XVII also break this link they do so in a transversal way and thanks to the location of the Albatajar creek, a viaduct or oversized bridge could be designed to preserve the free passage of wildlife. A similar situation occurred with sections XVIII and XIX. Finally, it should be noted that freeway section X intersects the wide links 10_17 and 10_19 (with high values of $\delta PC_{connector}$), and also occupies a large part of node 19. We therefore conclude that the best route would include freeway sections I, V, VI, VIII, VIII, XVI, XVII and XIX. We also estimate that wildlife crossing structures would be most effectively located on the 10_17 link (with the alternative of enlarging the viaduct in the Albatajar Creek) and the 23_31 link (1.5 km stretch of potential zone for its location).

3.4. Influence of applied link probability definition methodology in connectivity analysis

When we focused our analysis on the relative importance of links, only 13% of our links (69 out of 528 links) contributed to almost the whole $\delta PC_{connector}$ value (>97%) for both *LCPA* and *CMTC_wb* (see Fig. 11). The differences can be seen for the interval 1–13%, where the contribution of the links produced by *LCPA* had up to 8% higher values than *CMTC_wb*. It is also worth highlighting that in as many as 70% of the contributions of $\delta PC_{connector}$, a similar number of links were needed for both methodologies. In the case of the relative contribution of the nodes to $\delta PC_{connector}$, we observed higher values for inputs obtained by *CMTC_wb* methodology than *LCPA*: as much as 7% in the 80–90% interval of accumulated relative $\delta PC_{connector}$ contribution.

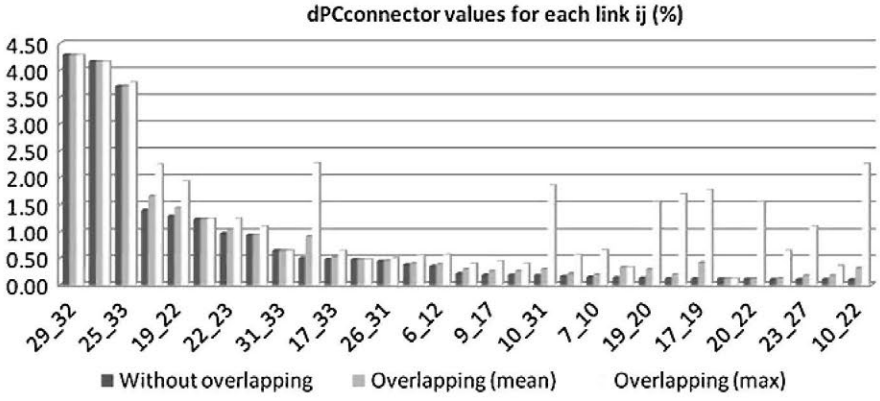

Fig. 9. Values of $\delta PC_{connector}$ for each link (those with $\delta PC_{connector}$ > 0.1) comparing values with and without overlapping effect. In the case of overlaps, mean and maximum values are shown.

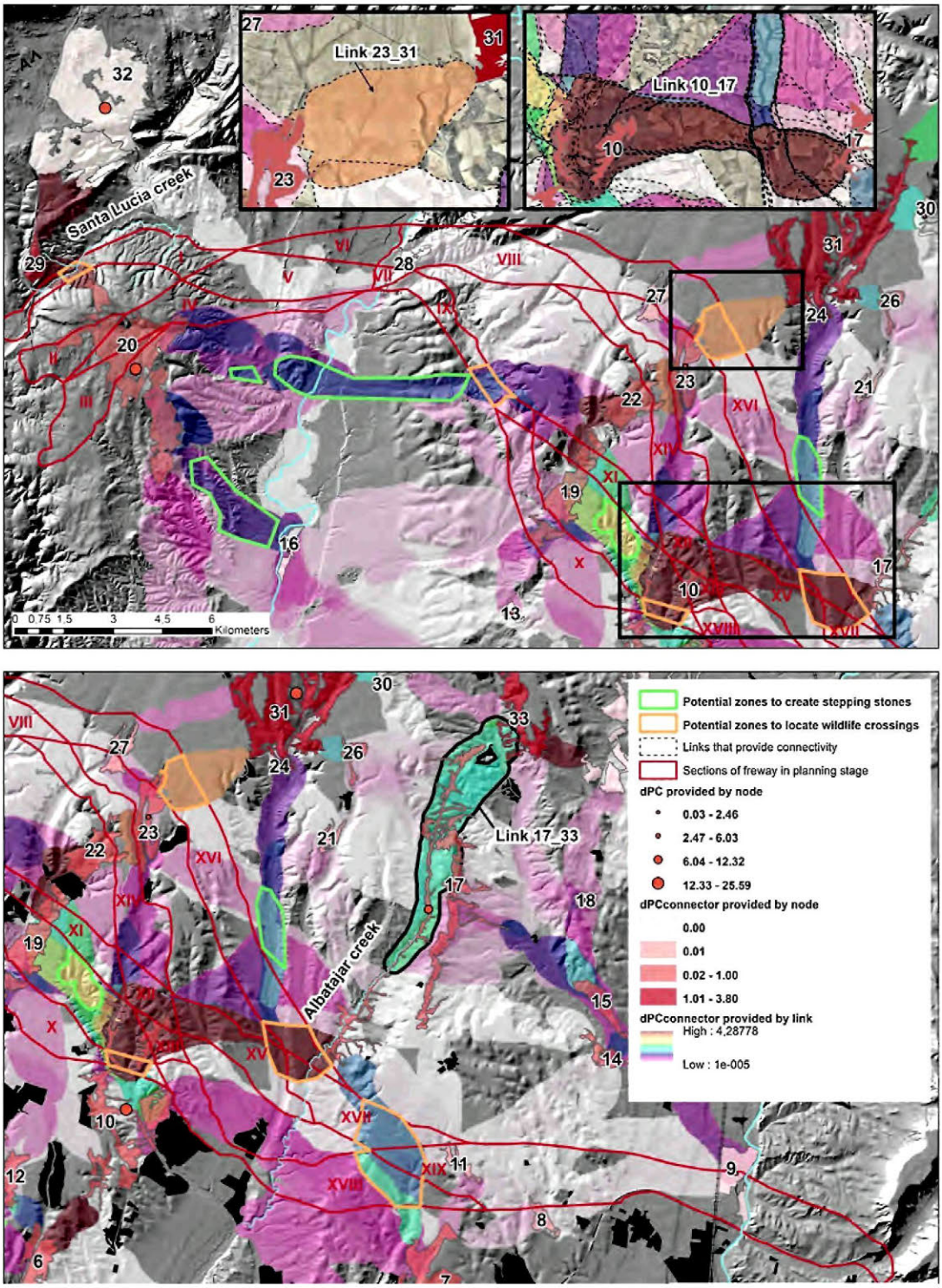

Fig. 10. Potential sites where wildlife crossings and oversized viaducts can be located in the different road corridor planning sections to maintain landscape permeability for wildlife passage.

For a single key element scale, we obtained minor differences in δPC values for nodes between *LCPA* and *CMTC_wb* to define link probabilities (see Fig. 12a). Among the 17 nodes with highest δPC values, only three nodes had differences over 5% (nodes 17, 32 and 33), with an average difference of 1.25% for all of them. In these three nodes, the percentage of contribution of each fraction (intra, flux and connector) was highly significant, highlighting the sharp increase in $\delta PCconnector$ in node 17 (see Fig. 12b and d).

With regard to the connectivity importance of links with higher values of $\delta PCconnector$, we found significant variations for four links (29_32, 29_20, 17_10, 17_33). It should be noted that the most important link obtained with the *LCPA* methodology (17_33) did not have high values with *CMTC_wb*. Furthermore, link 26_17 obtained a $\delta PCconnector$ value of 1.8% with *LCPA* and none with the *CMTC_wb* methodology. Inversely, we found the same situation for links 29_32 and 29_20.

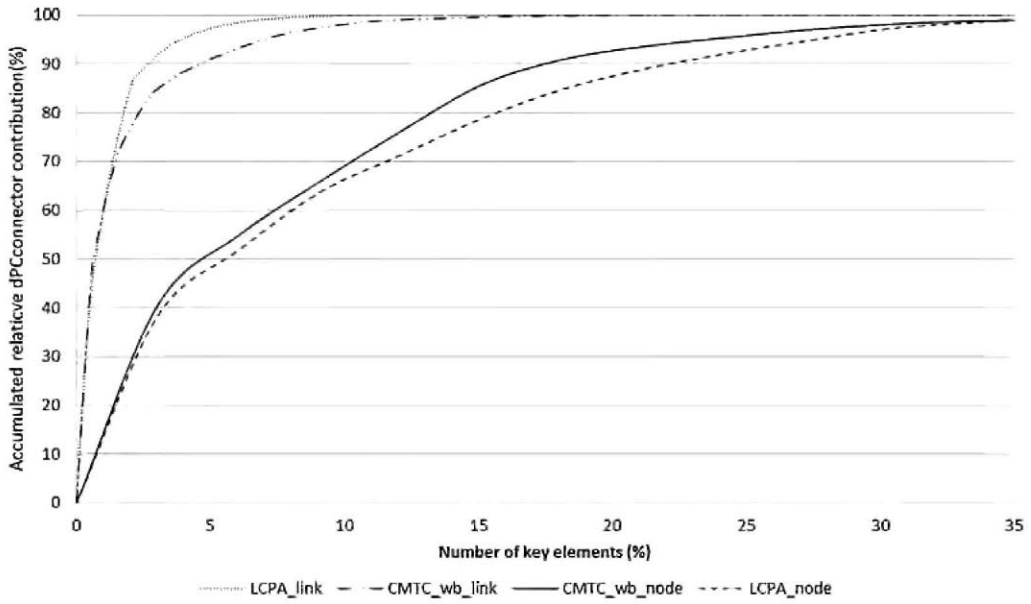

Fig. 11. Relative contribution of the top connecting key elements (nodes and links) as a function of the proportion of total number of links and nodes for the connectivity analysis performed by link characterization with *LCPA* and *CMTC_wb* methodology. The relative contribution was calculated as the ratio between the sum of the *δPCconnector* values for all the nodes and links in that set and the sum of the *δPCconnector* values for all the key elements in the study area.

4. Discussion and conclusions

Our proposed *CMTC_wb* methodology to define the connection probability of the links in our landscape graph as input to the landscape connectivity indicator *δPC* and its fractions is an interesting adaptation of *CMTC* (Pinto & Keitt, 2009). Wider corridors were obtained for the higher threshold values than least-cost path during the process of reclassifying cumulative cost distance distribution. Part of these corridors included the least-cost paths (see Fig. 6), but other alternative corridor branches were located far from the least-cost paths. Similar results were found by other authors (Theobald et al., 2011, 2012), who highlighted the difficulty of defining this threshold value in an ecologically representative way with minimum habitat requirements and ensuring the corridor has enough buffer area throughout its length to guarantee its viability (Bentrup, 2008). In our case, we iteratively and progressively increased this threshold value using natural breaks in the distribution of the cumulative cost friction values of each link in order to find corridors

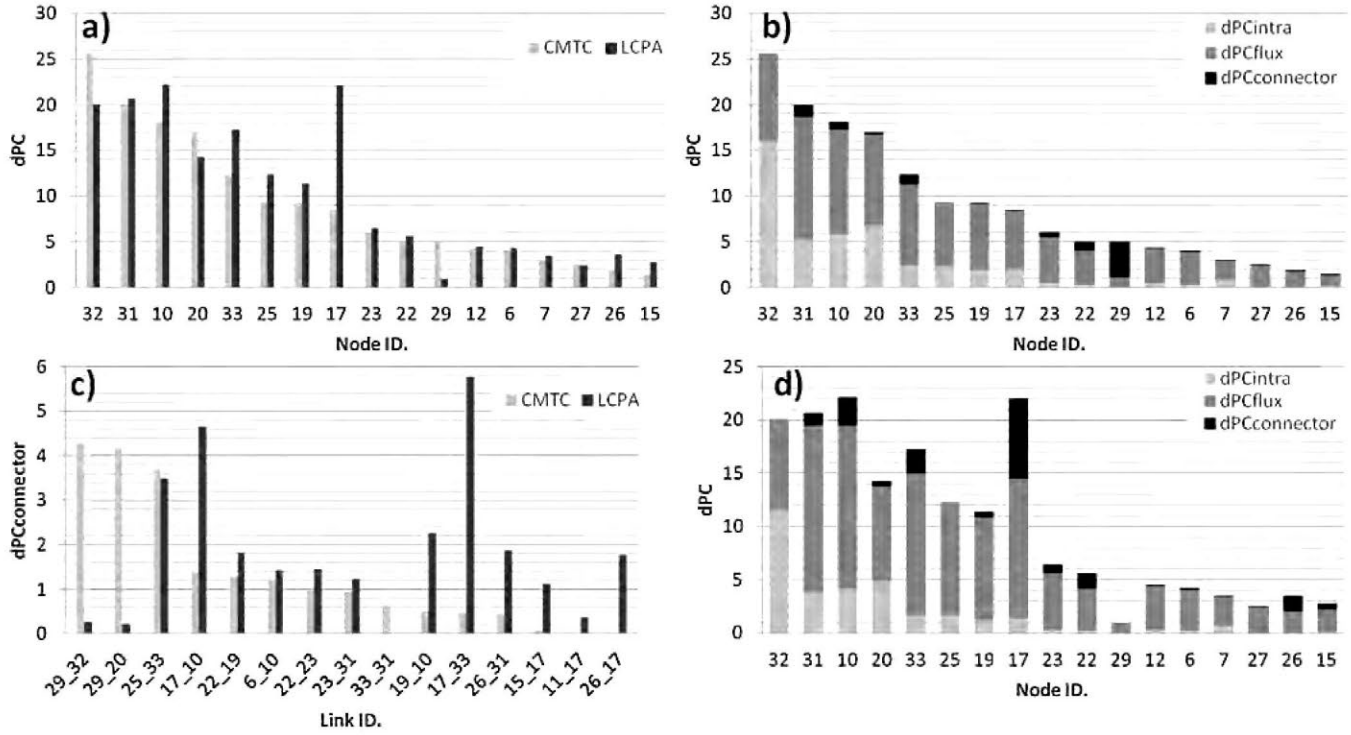

Fig. 12. (a) Comparison of the highest *δPC* values obtained per node depending on *CMTC_wb* or least-cost path methodology to define link probability connection for d_{ij} = 3.5 km. (b) Partial fraction contribution with links defined by *CMTC_wb*. (c) Comparison of highest *δPCconnector* values obtained per link depending on *CMTC* or *least-cost path* (*LCPA*) methodology to define link probability connection for d_{ij} = 3.5 km(c). (d) Partial fraction contribution with links defined by *LCPA* methodology.

without bottlenecks and a reduced cost. Our proposed methodology allows users to define as many natural breaks as desired in the analysis, making it a more flexible and detailed. Indeed, we believe our methodology extends and complements the methodology published by Theobald et al. (2006). In Theobald et al. (2011), the authors used *FunConn* tool (Theobald et al., 2006) to assess only the minimum (Q1) and 25th (Q25) percentile. In contrast, our study assessed 1000 natural breaks in a sensitive approach with smaller differences (mostly <1% of Co_{ij}) between two consecutive corridors defined by the *GAC* script. If the user increases the number of natural breaks in which the Co_{ij} distribution is divided, the difference in cumulative cost distance between two consecutive classes will decrease, making the analysis more detailed. One possible drawback is that more iteration may be needed among natural breaks to find a corridor without bottlenecks. In a subsequent step, we performed the analysis iteratively from the minimum natural break point (bv1) to the 22nd natural break point. The 22nd natural break point represented the threshold values where at least one path in each link (connecting a pair of nodes) had no bottleneck (see Appendix A, Fig. S1). In this process, higher natural breaks values produce a higher cumulative cost distance (see Fig. 7C) and thus less likelihood of being used by focal species. The degree of similarity of the landscape matrix composition to the optimum habitats in each case study will condition the maximum natural breaks that can be iterated in pursuit of the absence of bottlenecks. In a hypothetical scenario where corridors without bottlenecks can only be obtained with high values of natural breaks, and these are associated to zero probability of use by wildlife, this will imply that this landscape matrix is too anthropized to host corridors among nodes.

The results of our connectivity analysis concur with Gurrutxaga et al. (2011) and confirm that the δPC index and its fractions were able to emphasize areas thought to be important to network connectivity, even when the landscape was clearly fragmented. The median dispersal distance value of 3.5 km which obtained the highest δPCconnector values in our case (see Appendix A, Figs. S2 and S3) was similar to the dispersal movement capacity found by other authors between a range of 3–5 km in the colonization sequence of roe deer in Mediterranean landscapes (Acevedo et al., 2005; Acevedo, Real, & Gortázar, 2011) (see Table 1). Roe deer can therefore be seen as a potential focal species to take into account in connectivity analysis in fragmented Mediterranean landscapes. Species with medium dispersal distance abilities are seen to be very sensitive to the existence of habitat stepping stones (Acevedo et al., 2005). In our study, habitat patches located in the center of the study area (see Fig. 8), were found to be important stepping stones for maintaining landscape connectivity. These results should clarify which areas to preserve since their high δPCconnector values show an immediate decrease in connectivity when removed (Bodin & Saura, 2010).

Wildlife corridor boundaries were defined through a *CMTC_wb* iteration process in Geographic Information Systems (GIS), and their relevance in maintaining landscape connectivity was evaluated. This allowed us to perform a raster sum operation for each corridor to establish the overlapping areas with higher values in each corridor (see Fig. 8). This type of result could equally well be achieved with least-cost path methodology with buffer operations around the least-cost path lines, but would not be ecologically based on the cumulative cost distance. As can be seen in Fig. 9, several corridors obtained little connectivity importance if they were assessed in isolation, but had a high δPCconnector pixel value as a result of the overlapping operation. It is worth mentioning the high potential of these areas with high connectivity values for the creation of new stepping stones to maintain landscape connectivity for roe deer. Similar results were obtained depending on the inputs provided by the *LCPA* and *CMTC_wb* methodologies to define links (see Fig. 11). However, only with the *CMTC_wb* methodology was it possible to identify these potential areas to create new stepping stones with a clearly delimited physical area.

In the particular case of impact assessment applications such as Environmental Impact Assessment and Strategic Environmental Assessment, these connectivity elements could be regarded as important for biodiversity at the genetic level (Zetterberg et al., 2010). In our case study, we were able to discriminate among different freeway layout alternatives according to how they affected the nodes and links in terms of maintaining global landscape connectivity. Moreover, as part of the restoration and compensatory measures planned for the new freeway, we were able to pinpoint potential areas where wildlife crossings (underpasses or overpasses) should be installed to reduce barrier effects (junctions between road sections and wildlife corridors) and locate areas for restoration of natural habitats as stepping stones (potential habitat banking zones). These measures can be classified as mitigation (steps to minimize, rectify and reduce adverse impacts) and compensation measures (the replacement of natural habitat that generally takes place elsewhere) (Cuperus et al., 1996; Cuperus, Canters, Udo de Haes, & Friedman, 1999). For the sake of comparison, prior to our study the δPC index (Saura & Pascual-Hortal, 2007) was applied to assess the fragmentation and barrier effect of road networks on landscape connectivity (Fu et al., 2010; Gurrutxaga et al., 2011). Both these studies used least-cost path as input, and thus did not have the advantage of multiple paths as potential links, reducing the potential restoring due to not detailed physical extent of each wildlife corridor. Similar drawbacks can be seen in Girardet et al. (2013), where connecting links were defined by the Graphab 1.0 software. Another potential application of our results is for use as a thematic map to create a relative cost distance raster from which alternative layouts of potential road corridors could be defined through the least-cost path algorithm. Because the algorithm would assign an extra cost to pixels with a greater importance to connectivity, the new road layout could avoid them and contribute to achieving a road layout design with less impact. Good examples of planning methodologies aimed at reducing the impact of new transport infrastructure can be found in the literature (Atkinson, Deadman, Dudycha, & Traynor, 2005; Rapaport & Snickars, 1999).

The main limitation of our proposed methodology is that it requires additional territorial (detailed landscape structures maps) and ecological (dispersal distance and movement probability, boundary response, path shape, etc.) information, as well as a cost distance raster validation through data capture on actual movement paths and movement risks in the landscape, especially in human-altered landscapes (Fahrig, 2007). Field data collection may be required depending on the desired level of detail of the wildlife dispersal model. The inclusion of *CMTC_wb* methodology can reduce the barrier effect when tracing road layouts, especially if the analysis is focused on ranges of dispersal distances where there is a greater reliance on the key connector elements and the permeability of the landscape (Saura & Rubio, 2010). We believe our methodology to be a useful tool for environmental impact assessment studies for proposing ecological mitigation and compensation measures in linear transport infrastructure projects. Although our goal was to define wildlife corridors with multiple paths and without bottlenecks and to evaluate them with a connectivity index, our results suggest that the least-cost path is a good approach to assess overall connectivity, as can be seen from the scant variations of 7% in the accumulated relative $\delta PC_{connector}$ contribution between *LCPA* and *CMTC_wb* (see Fig. 11), although revealing major variations at the single corridor scale (four links and three nodes, see Fig. 12). The main cause of these variations is that *LCPA* overestimates the corridors' probability as neither bottlenecks or alternative paths are taken into account. In consequence, corridors defined by *LCPA* obtained higher values of $\delta PC_{connector}$

with fewer links than corridors defined by *CMTC_wb* (see Fig. 11 and Section 3.4), but this could be unrealistic. In conclusion, we propose using *CMTC_wb* methodology in connectivity studies, especially in fragmented landscapes as in our case study, where the *LCPA* methodology could ignore strong local variations in cost matrix grids for wildlife dispersal movements.

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Manuel Loro is a PhD student and a researcher at the Department of Transport and Territory in the Civil Engineering School of the Technical University of Madrid (UPM). He is also member of Transyt (Transport Research Center-UPM). He is developing his PhD on Environmental Impact Assessment and GIS planning. He focuses his research on GIS applications to reduce environmental impacts, especially associated to new roads building.

Emilio Ortega, PhD, is an assistant professor of GIS at the Department of Forestry and Environmental Engineering and Management in the Forestry Engineering School of the Technical University of Madrid (UPM). He is also member of Transyt (Transport Research Center-UPM). His research topic is focused on territorial transport planning and strategic environmental assessment.

Rosa Arce is an associate professor at the Department of Transport and Territory in the Civil Engineering School of the Technical University of Madrid (UPM). She has over 25 years of EIA experience as a project manager, and as a specialist advisor–peer reviewer in such areas as impact prediction and interpretation methodology, alternatives evaluation and the integration of sustainability in decision making. She has wide experience in applied EIA practice and research, taught EIA at the graduate and undergraduate levels, and published widely in the field.

Davide Geneletti is an associate professor at the Department of Civil, Environmental and Mechanical Engineering, University of Trento, Italy. His research topics are focused on assessing the environmental effects of spatial plans and large infrastructure projects and interacting ecological concerns in planning, through the use of information of ecosystem services.